Effects of Spatial Resolution and Cell Shape on Management Results from an Individual-based Salmon Spawning Model

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I.   Introduction

A.   The resolution issue

Selecting an appropriate spatial resolution is a key step in ecological modeling, typically described as one of the first important decisions in designing a spatially explicit model (e.g., Grimm and Railsback 2005; Manly et al. 2002; Starfield and Bleloch 1986). "Spatial resolution" refers to how finely space is depicted. Most spatially explicit models represent space as a collection of "cells" that each represent an area of habitat; habitat variables differ among cells, but variation within each cell is neglected. Most commonly, the entire space is represented as a grid of square cells, but some models (including the one used here) represent space as a mesh of irregular polygons. High-resolution ("fine-grained") models use many cells that each represent a small area, while low-resolution ("coarse-grained") models use fewer and larger cells.

There are several reasons why a model's spatial resolution is important. First, practical reasons include that higher-resolution models tend to have higher costs in input data requirements and computation. When cell variables are given values from field observations, higher resolution can mean that field observations must be closer together. This difference can be especially expensive if low-cost observation methods (e.g., remote sensing) cannot provide the necessary resolution, so higher-cost methods (e.g., manual observations on the ground) are required. Computational effort for a simulation model often increases more than linearly with the number of cells, and the number of cells decreases with the square of cell width. Hence, the computational cost of higher resolution can be significant when large areas are modeled. However, modern data collection technology and computer power are reducing the importance of these practical considerations.

A second reason for the importance of resolution is that it determines a model's ability to capture the spatial variability of the systems being modeled. Because habitat variation is neglected within a cell, larger cells are less able to depict realistic detail. But this does not mean higher-resolution models are necessarily more useful, accurate, or scientific: the main purpose of a model is to simplify away unnecessary detail while capturing the most important variability. Unnecessarily high resolution can make models less accurate and harder to use. (Analysts of remote sensing data have long realized that too-high resolution can make it harder, not easier, to categorize an image into meaningful information.)

The potential for scale artifacts are a third reason to pay attention to spatial resolution in ecological models. Artifacts are strong effects on results that arise from the details of a model's design instead of from the underlying ecological processes and variables. DeAngelis and Petersen (2001) illustrated such a scale artifact in a mechanistic predation model. The model represented consumption of prey fish by predator fish that were each confined to one cell of a reservoir model. Cell size therefore determined the area a predator fed over, so predicted predation rates depended strongly on the model's spatial resolution.

The final, and perhaps most important, reason why spatial resolution is important is that ecological relations can change as spatial scale changes (Levin 1992). This realization was a fundamental step forward in ecology and the subject of a great deal of research, especially in the 1980s and 1990s, that produced many examples of relations (such as those between habitat and population density) that vary with scale (e.g., Bissonette 1997; Crawley and Harral 2001; DeCesare et al. 2012; Poff and Huryn 1998; Scott et al. 2002). An example familiar to stream fish biologists is velocity selection by drift-feeding fish such as

trout. These fish often shelter in the low-velocity eddy behind cover (e.g., a boulder) while feeding on drift carried by the adjacent high velocities (Fausch 1984). Hence, when observed at a scale of a few cm, the fish is selecting low velocity; but observed over the entire area used for feeding it is selecting a much higher velocity. Similarly, stream fish can appear to avoid dense cover over short distances (presumably because it interferes with visual feeding), while strongly selecting for cover over longer distances (that are still close enough for the fish to reach quickly when a predator is detected).

What is an appropriate resolution for an ecological model? Again, there are both practical and ecological factors that matter. Data resolution can be an upper limit on model resolution, if it is not practical to collect additional data at higher resolution. (Data at a higher resolution than desired can generally be aggregated to coarser grain, though aggregation can be expensive and inconvenient.) Habitat variability can be another factor: there is no need, for example, for small grid cells when habitat variables change by important amounts only over long distances; but if important changes in habitat occur over short distances then smaller cells are needed to capture the changes.

The ecological factors affecting choice of spatial resolution can be less clear and obvious yet even more important. Key ecological considerations include what activities or processes are being modeled, what distances those activities or processes are carried out over, and the model's time step. Returning to the drift-feeding fish example, suppose a model is designed to represent how water velocity affects food intake and growth (which depends on swimming effort as well as food intake). If the model is so fine-grained that it captures the different velocities in and outside the fish's velocity shelter, then modeling movement of a fish among cells would require representing such detailed processes as when the fish detects prey and how much time it spends pursuing prey in the high-velocity cells vs. waiting in the low-velocity cell. Obviously, such a model would require a very short time step to capture such behaviors. Alternatively, a coarser model with cell size approximating the entire area used by a feeding fish could use simpler approximations and parameters to represent the combined effects of feeding in a high-velocity cell that also contains velocity shelter (the approach of the model used here).

Spatial resolution has been a contentious issue in models applied to streamflow management (Durance et al. 2006; Railsback 1999; Railsback 2000; Williams 2001). A root cause of this contentiousness is that the widely used PHABSIM model (Bovee 1982; Bovee et al. 1998) neglected spatial resolution issues and made several resolution-related errors. Spatial resolution of traditional PHABSIM applications was typically based on guidance for measuring stream flow (e.g., the rule of thumb to use 20 measurements across a stream channel) instead of considering either habitat variability or biological considerations such as the area used by individual fish. The biological components of PHABSIM ("suitability criteria" that are essential habitat selection functions) are typically based on observations at a much finer resolution than the physical habitat component. The drift-feeding example above illustrates the kinds of errors that this resolution mismatch can induce (Railsback 1999). Durance et al. (2006) reviewed hundreds of instream flow studies and concluded that spatial scale issues were widely neglected to the detriment of study reliability. In contrast, there is now a substantial literature on how to properly address spatial scale issues in habitat selection and related models for terrestrial wildlife; e.g., Betts et al. 2006; Boyce 2006; Corsi et al. 2000; Pribil and Picman 1997. Dunbar et al. 2012 at least discuss this issue in relation to instream flow modeling.

B. Study objectives and general approach

Our primary objective is to examine how spatial resolution—cell size—affects management decision-support results from an individual-based salmon model. The model, inSALMO, simulates salmon spawning, egg incubation, and juvenile rearing as affected by habitat variables such as flow, temperature, and turbidity regime; channel shape and hydraulics; and availability of spawning gravel and cover for feeding and hiding. For example, how does the model-predicted relationship between base flow and spawning success vary as cell size is varied? A secondary objective is to compare two approaches to habitat cell delineation: irregular polygons that reflect habitat variability versus square grid cells that do not. Irregular polygons require more effort to define and use. Square grid cells are appealing because they require virtually no effort to define, and offer the potential to use remotely sensed data to evaluate habitat variables without the need for averaging or interpretation into other shapes, a source of error and uncertainty. Square grid cells also greatly reduce the conceptual and computational complexity of simulation models and allow use of grid-based software platforms such as NetLogo (Wilensky 1999). Some stream hydraulic models use irregular polygons while others use square or "warped square" grid cells.

Our approach was simply to run inSALMO using ranges of spatial resolution in otherwise-identical simulation analyses, to see how results differ with cell size. Three levels of resolution (fine; medium; coarse) were used. One set of experiments used expert-generated irregular polygons, and a second used a regular grid of square cells. We identified differences among these scenarios and investigated their causes, to draw conclusions about (a) how and why model results (and management recommendations based on them) vary with spatial resolution, (b) what resolutions seem to provide a good compromise between cost and model credibility, and (c) the tradeoffs in using irregular vs. square cells, such as how many more square cells are needed to produce results similar to those of irregular polygons.

II. Methods

A. Model summary

The model, study sites, and decision-support simulation experiments used here were identical to those of a previously published application of inSALMO (Railsback et al. 2013; Railsback et al. 2011 provides a complete model description), with exceptions noted below. inSALMO is an individual-based simulation model of the freshwater life stages of salmon, from when adults arrive from the ocean through spawning, egg incubation, fry emergence and rearing, until juveniles migrate downstream out of the simulated stream reaches. The model, like its predecessor stream trout models, was designed primarily as a river management decision support tool, and makes testable predictions of how population characteristics (abundance, biomass, habitat selection, migration timing, etc.) respond to physical habitat (Railsback and Harvey 2002; Railsback et al. 2005, 2009, 2011, 2013).

inSALMO operates at a daily time step, and can simulate one or several sequential years. Habitat in inSALMO is represented at two scales: reaches and cells. A simulation can include one or more reaches, which are contiguous lengths of stream. Each reach is depicted as a collection of cells. Reach variables include daily flow, temperature, and turbidity, which are assumed uniform among the reach's cells. Cells have unique values for variables including depth and velocity (calculated from flow using an external hydraulic

model), food availability, spawning gravel area, area providing velocity shelter for drift-feeding fish, and distance to hiding cover. The locations of individual fish are tracked only by which cell the fish are in.

Three kinds of objects in the model represent salmon. At the start of a simulation, *adults* are created as if they were appearing in spawning reaches after migration from the ocean. Adults then spawn and create *redds*, objects representing a nest of incubating eggs. After a temperature-dependent incubation time, surviving eggs "emerge" by turning into *juveniles*. The juvenile objects are actually "superindividuals" that each represent 10 real salmon fry/pre-smolts. Eggs are subject to several kinds of mortality, including superimposition when other redds are created in the same cell, and temperatures either above or below an optimal range. Juveniles select habitat by attempting to move to cells (within a radius that increases with fish size) that provide high "expected fitness", a combination of growth and predation risk. Both growth and risk depend on habitat variables, and grow is also affected by competition among juveniles for food. Habitat selection is modeled assuming a size-based dominance hierarchy: the largest juveniles select habitat first, and smaller ones have access only to resources (food, velocity shelter) not used by bigger individuals. Juveniles migrate downstream if no available cells offer an acceptable expected fitness, with the threshold expected fitness to stay increasing with fish size (so fish become more willing to move downstream as they grow and approach smolt size).

Our simulations use two reaches on lower Clear Creek, Shasta County, California (described in more detail by Railsback et al. 2013). Clear Creek is a moderate-sized (watershed area: 65,000 ha) stream with flows and temperatures controlled by the upstream Whiskeytown Reservoir. Site 3A underwent extensive restoration that widened the channel, added bends and habitat structures, and added spawning gravel. Site 3C was a control site for the habitat restoration program, and is substantially narrower, straighter, faster, and more uniform than 3A, with somewhat less spawning gravel.

The model and input used in this study differ from that described by Railsback et al. (2011; 2013) in only a few ways. We included minor changes to model assumptions and parameters that resulted from calibration and validation, as documented by Railsback et al. (unpublished). We also developed new habitat input for the two study sites, as described below at Section IID.

B.   Expected effects of spatial resolution

Spatial resolution and its potential effects were considered carefully in the design of inSALMO, and the model was designed to be insensitive to spatial resolution to the extent possible. For example, fish can use hiding cover over longer distances than they feed over (a frightened fish may flee several meters to cover). This difference was accommodated by describing cell hiding cover availability as a typical distance a fish in the cell would travel to find cover; this variable is independent of the cell's size.

Redd superimposition is one important process potentially sensitive to cell size, though inSALMO was designed to reduce this sensitivity. inSALMO assumes that a redd is subject to a risk of eggs being killed by superimposition whenever another redd is created in the same cell. However, that risk decreases as the cell's area of spawning gravel increases; spawners are assumed more likely to put redds in cells with more gravel. Hence, dividing a cell of 50% spawning gravel into two cells with 0 and 100% gravel would produce the same amount of superimposition—*if* the same number of redds are created in the two cells. However, a spawner places its redd in the cell that (a) has highest "suitability" (a function of

depth and velocity as well as gravel availability), and (b) is not guarded by a female adult that previously spawned in the cell. Dividing spawning habitat into smaller cells could increase superimposition by causing more adults to spawn in the now-smaller cells with absolutely best suitability. The unguarded area in such cells can be quite small, making superimposition very likely.

Competition for food is a second process likely sensitive to cell size, because the number of fish feeding in a cell is an integer. The density of fish that a cell can support therefore can depend on its size. Imagine a cell containing just enough food to sustain three juvenile superindividuals (to reduce computations, inSALMO represents juvenile salmon as "superindividual" objects that each represent multiple—typically 20—individuals). If the cell was divided into two equal cells, each would sustain only one juvenile (there is no such thing as a half-fish to eat the food remaining in each cell). Therefore, the same area would sustain 2/3 the number of fish as the original cell. Dividing the original cell into four would result in each cell having ¾ the food needed to sustain one juvenile, so the habitat would support none. This effect of cell size clearly also interacts with the superindividual size (number of juvenile salmon represented by one superindividual). To reduce (but not eliminate) this artifact, we generally tried to make cells larger than about 1 m^2 in area, even for the finest-resolution scenarios.

Finally, spatial resolution is expected to affect the availability of especially good patches of habitat, where hydraulics and cover variables produce high growth and relative safety from predation. The availability of such patches strongly affects the (typically small) number of salmon juveniles that survive and grow before migrating downstream. For newly emerged juveniles, the ranges of depths and velocities providing good growth and survival are narrow, and often are available in small zones such as channel margins. As cell size increases, averaging of depth and velocity is likely to eliminate small areas of especially good habitat. On the other hand, averaging into larger cells could occasionally create a large cell of especially good habitat out of smaller cells with velocities too high and too low.

C.   Simulation experiments

We used inSALMO as parameterized for fall-run Chinook salmon in Clear Creek by Railsback et al. (2013; unpublished), simulating water years 2004-08 (from arrival of adults in October 2003 through outmigration in the summer of 2008). Like Railsback et al. (2013), we used inSALMO's "Limiting Factors Tool" which automatically generates and executes simulation experiments examining sensitivity to a variety of potentially manageable factors such as base flow, spawning gravel availability, and availability of cover for drift-feeding and predator-avoidance.

The model results we analyzed are the number of "large outmigrants", which are juveniles that survived to migrate downstream out of the two simulated reaches and grew to at least 5 cm fork length before doing so. The vast majority of juvenile salmon from Clear Creek (simulated and real; Railsback et al. 2013) migrate downstream immediately after emerging, so their numbers do not reflect juvenile rearing conditions. The number of large outmigrants, though, is an indicator of habitat quality for juvenile rearing as well as spawning and egg incubation.

To clarify the relation between spatial resolution and superindividual size (Section IIB), the Limiting Factors Tool's base flow experiment was repeated using superindividual sizes of 1, 2, 5, 10, 20, and 50. These experiments used only site 3A and the three polygon-

based representations of space (resolution scenarios P-FINE, P-MED, and P-CRS, explained below).

D.   Alternative representations of space

We simulated six spatial resolution scenarios. All were developed from the same set of information, developed by the US Fish and Wildlife Service as part of instream flow and habitat restoration studies (Gard 2006; USFWS 2005, 2006). This information included cover and substrate observations and hydraulic simulations from a finite-element hydrodynamic model (River2D; Steffler and Blackburn 2002), both conducted at a fine resolution. River2D was used to model depths and velocities at each node of an irregular polygon mesh that averaged one node per 0.9 m^2 at both sites. Substrate and cover observations were made at the same nodes. Even our finest-resolution scenario therefore required aggregation of hydrodynamic model results and field observations into larger cells.

Three scenarios used irregular polygons, the standard approach for inSALMO. The irregular, fine-resolution scenario (designated "P-FINE") used polygons delineated by hand by a fish biologist (J. White) familiar with the study sites. Polygons were drawn in a geographic information system (GIS) using depth contours and maps of habitat variables (generated from the node observations described above) as reference information. The goal of polygon delineation at this resolution was to capture as much of the site's habitat variability as possible while keeping cells no smaller than ~1 m^2 (estimated to be a minimum area to sustain at least one simulated juvenile superindividual, although the actual area needed to sustain one superindividual depends on depth, velocity, temperature, turbidity, and fish size) while not making cells smaller than necessary to represent larger areas of homogeneous habitat. The resulting polygons tended to be especially small and irregular in shape along the channel margins and banks, where bed elevation and velocity gradients tend to be high and cover relatively common.

The medium-resolution irregular polygons (scenario P-MED) were created by manually aggregating the P-FINE polygons into cells approximately four times larger. In the GIS, cells were merged with the most-similar adjacent cells, using the same information (depth contours, etc.) as in their original delineation. The same process was repeated to create the coarse-resolution polygons (scenario P-CRS).

The square cell ("grid cell") scenarios were created using a River2D tool that exports depths and velocities on a grid of points, with the user selecting the point spacing. We treated each such point as the center of a cell, with cell depth and velocity spatially averaged from the original high-resolution irregular mesh. The three square cell scenarios (designated S-FINE, S-MED, and S-CRS) used cell sizes of 2 m (so cell area is 4 m^2), 4 m (16 m^2 area), and 6 m (36 m^2 area). One-meter cells proved computationally infeasible: approximately 17,500 cells would be required for site 3A. Along the channel margins, cell boundaries were clipped to include only the area within the boundaries simulated in River2D, and cells were excluded if less than half their area fell outside those boundaries.

Once the cells were delineated, their static habitat variables (representing the fraction of cell area providing velocity shelter and spawning gravel, and a characteristic distance to hiding cover) were calculated from the substrate and cover variables observed at the hydraulic model nodes. The methods for calculating these cell habitat variables are described by Railsback et al. (2011; submitted).

III.   Results

A.   Habitat maps

The six habitat scenarios are illustrated in Figure 1 and Figure 2, with statistics at Table 1. For fine and coarse resolutions, the irregular polygon cells are approximately 2-3 times larger and correspondingly less numerous. At the medium resolution the size and number of cells differs less between irregular and square cells.

Table 1. Characteristics of the resolution scenarios.

Site	Resolution scenario	Number of cells	Mean cell area (m^2)
	P-FINE	1371	12
	P-MED	635	25
3A	P-CRS	189	85
	S-FINE	4320	3.9*
	S-MED	1090	15.4
	S-CRS	476	34.4
	P-FINE	825	9
	P-MED	418	17
3C	P-CRS	95	74
	S-FINE	1373	3.8*
	S-MED	438	15.1
	S-CRS	199	32.7

*Mean areas of square cells are less than the nominal areas of 4, 16, and 36 m^2 because cells along channel margins were trimmed of areas outside the simulated channel (Section II.D).
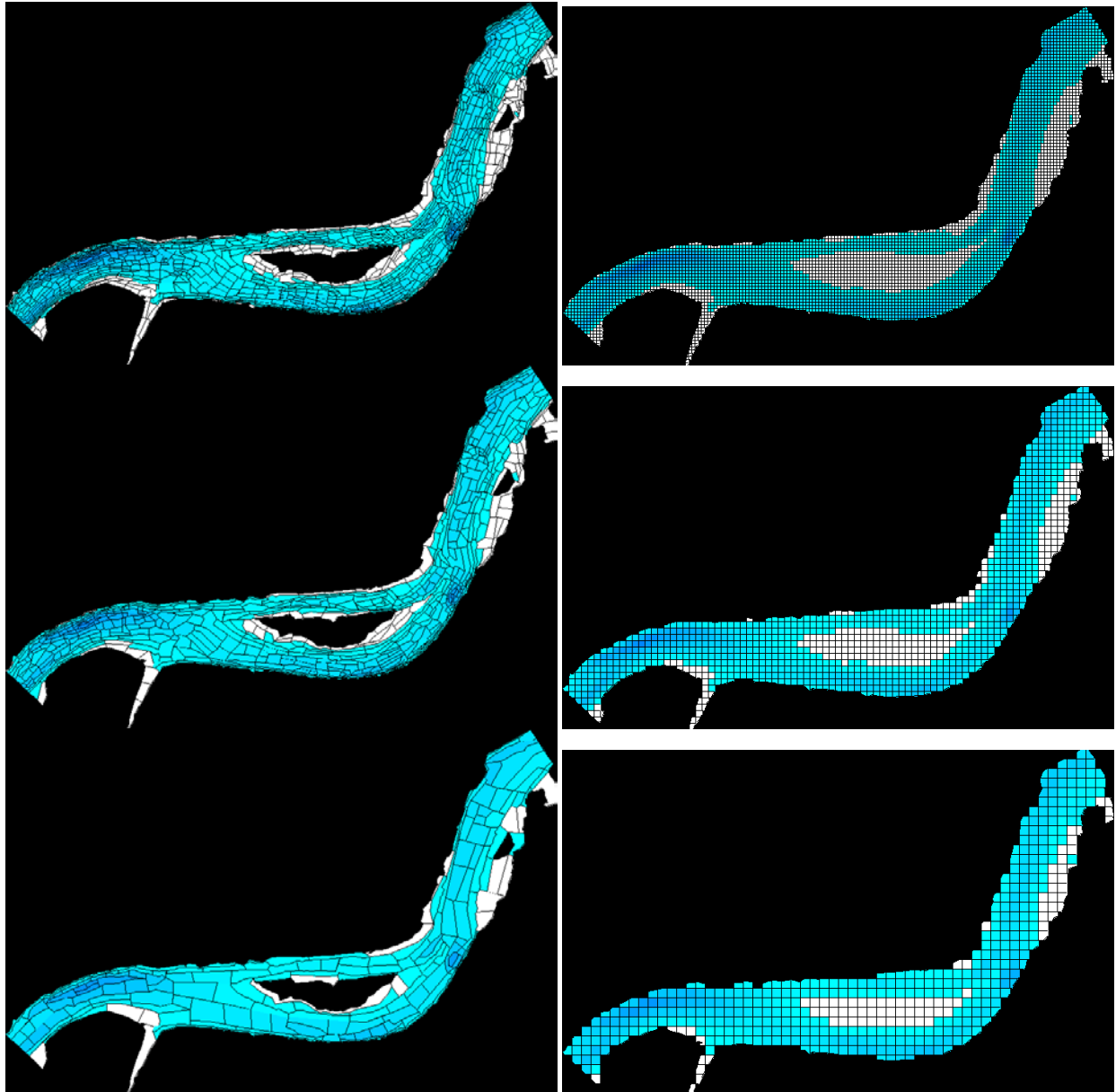
Figure 1. Resolution scenarios for site 3A. Left: irregular polygons; right: square cells. Resolution decreases (fine, medium, coarse) from top to bottom. Shaded cells contain water at a typical base flow of 6.2 m³/s. Shading reflects cell depth, with darker cells deeper.
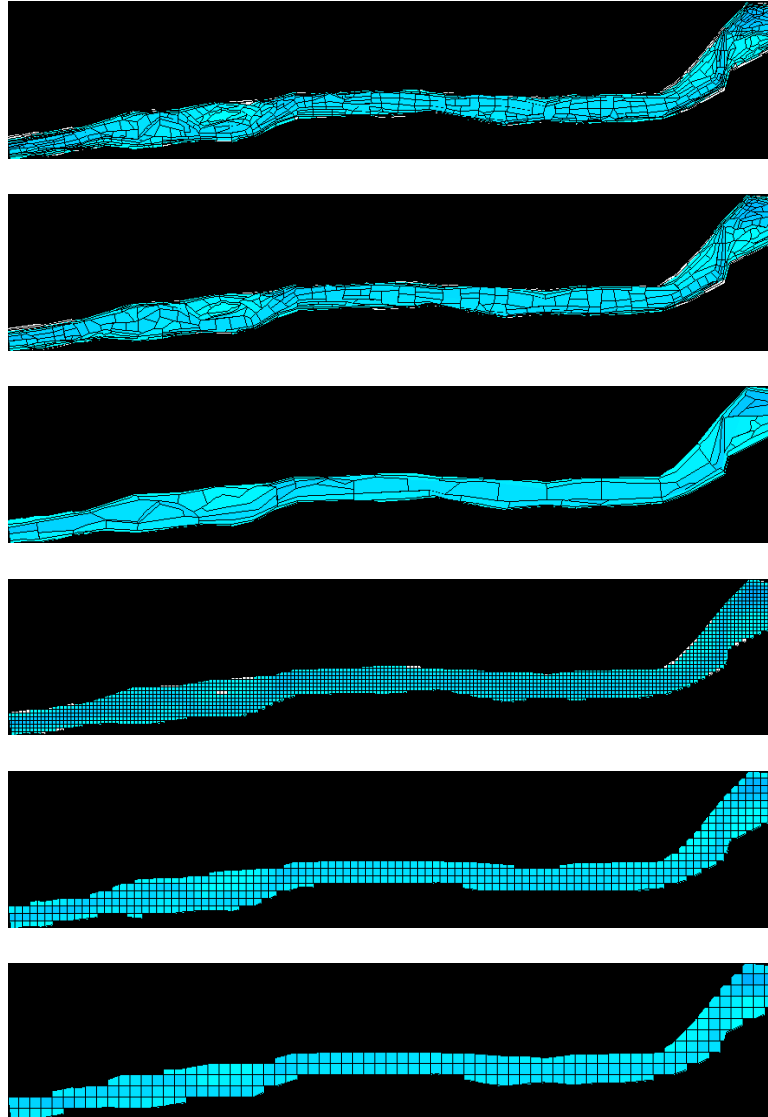
Figure 2. Resolution scenarios for site 3C. Format as in Figure 1, except that the three irregular polygon scenarios appear above the square cell scenarios.

Depth and velocity distributions for irregular polygon scenarios at a typical flow (left panels of Figure 3, Figure 4) indicate that fine- and medium-resolution produce very similar hydraulic conditions, while the coarse-resolution scenario tends to produce less area with depth and velocity less than about 40. For the square cell scenarios, (right panels of Figure 3, Figure 4), each decrease in resolution produces less area with low depth and velocity. The loss of slow, shallow habitat with decreasing resolution is especially clear at site 3C.
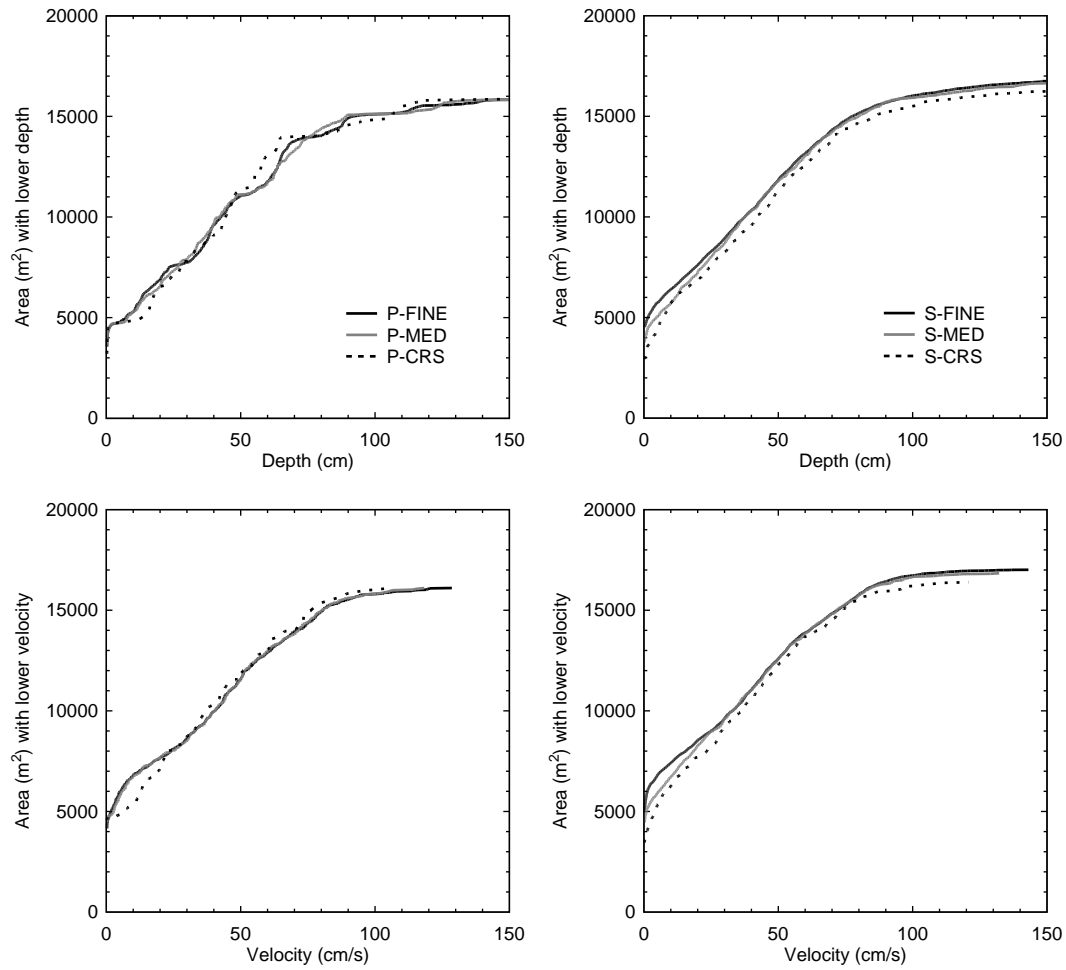
Figure 3. Depth and velocity distributions for site 3A, at a typical base flow of 6.2 m³/s. Left: irregular polygon cells; right: square cells. The Y axis is the site area with depth (velocity) less than the value on the X axis. The Y axis value at depth (velocity) = 0 represents cells that are not submerged at this flow.
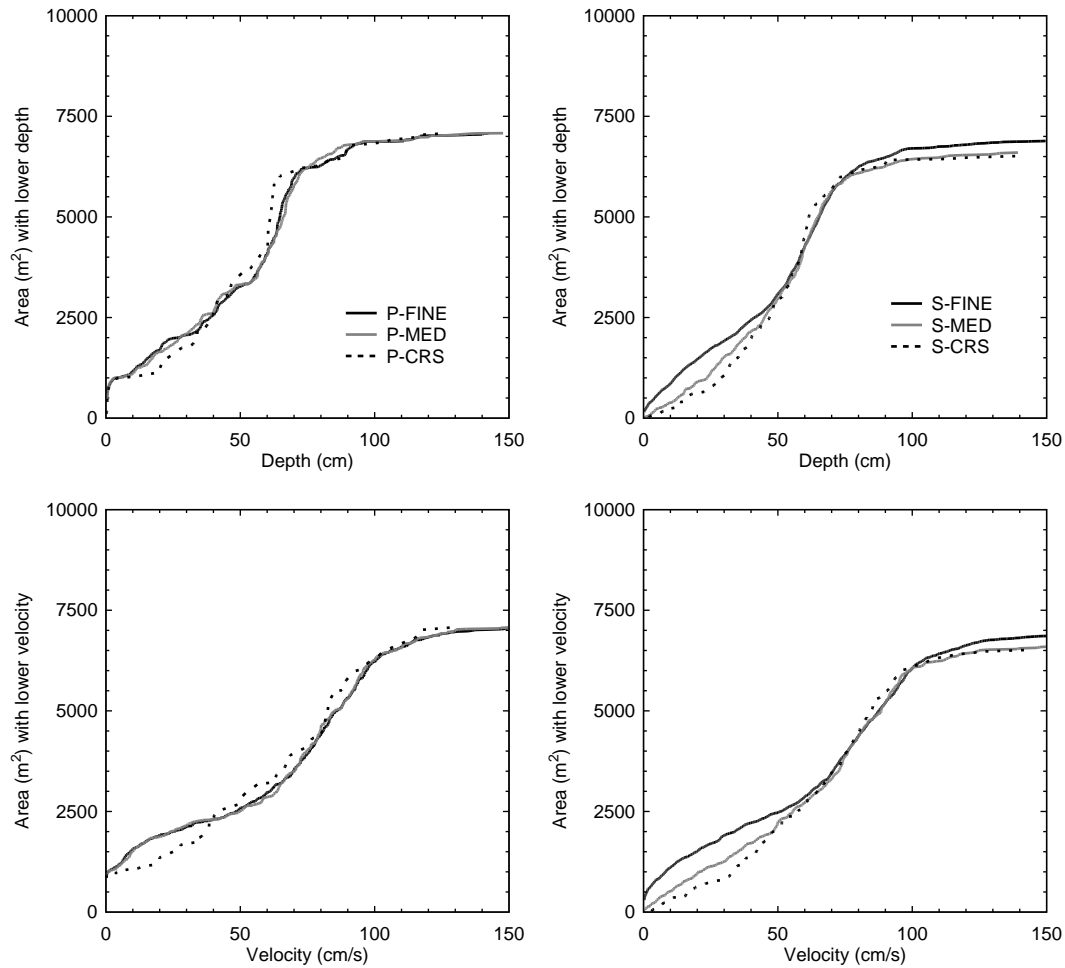
Figure 4. Depth and velocity distributions for site 3C. Format as in Figure 3.

B. Simulation experiments

The simulation experiments examined how the sensitivity of simulated production of large outmigrants to management variables depends on spatial resolution. The management variables included base flow, food availability, and hiding cover (Figure 5); number of spawners, availability of spawning gravel, and availability of velocity shelter (Figure 6); and piscivory risk, susceptibility of redds to scouring, and winter water temperature (Figure 7). In general, results from fine-, medium-, and coarse-resolution simulations produced similar trends (or lack of trends), although the magnitude of predicted large outmigrant production varied among resolutions. The most striking exception to this generality is the response to base flow (top panels of Figure 5): the P-CRS scenario produced different trends than the others, and at site 3C the square cells produced different trends than the irregular polygons.
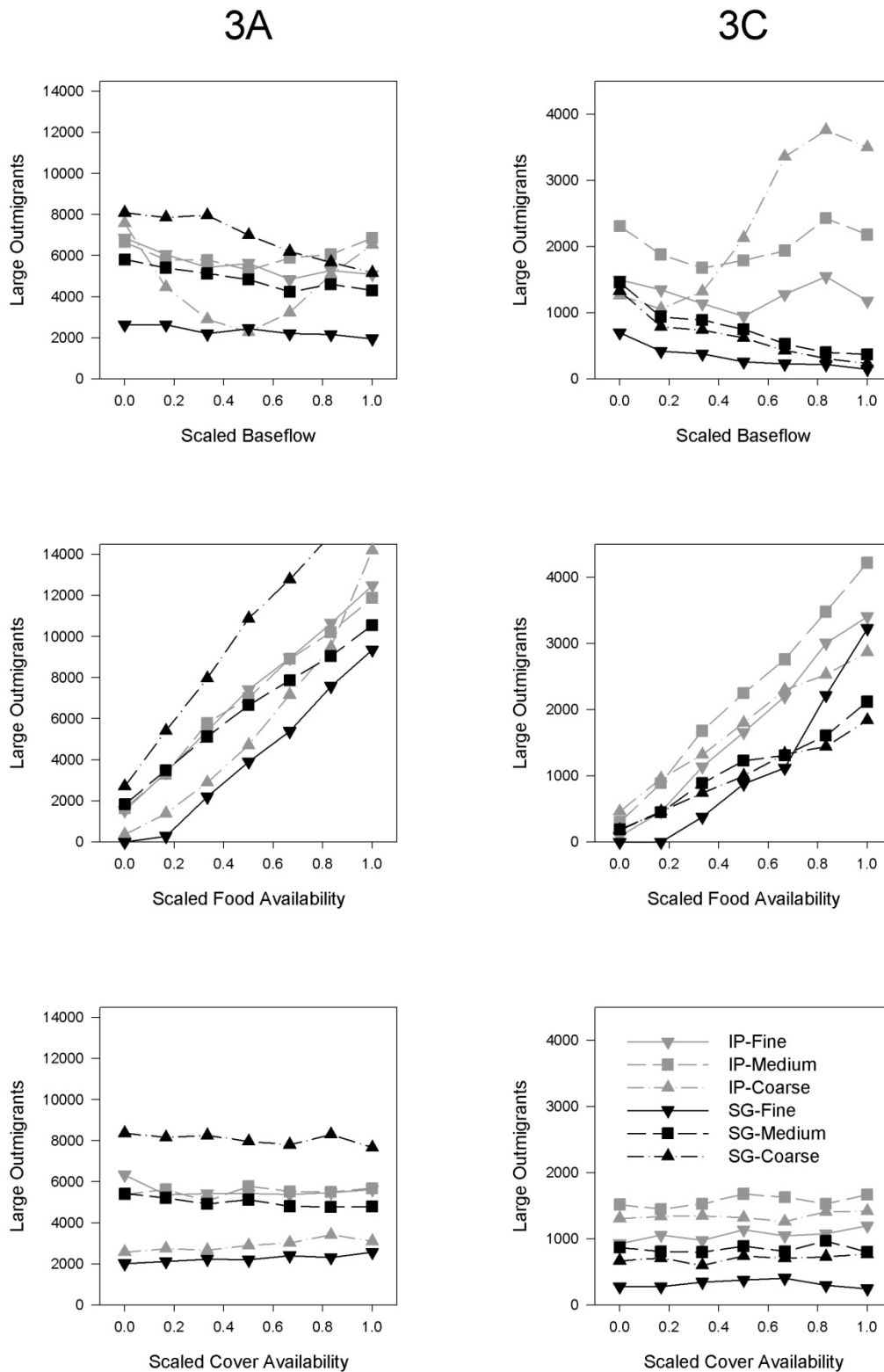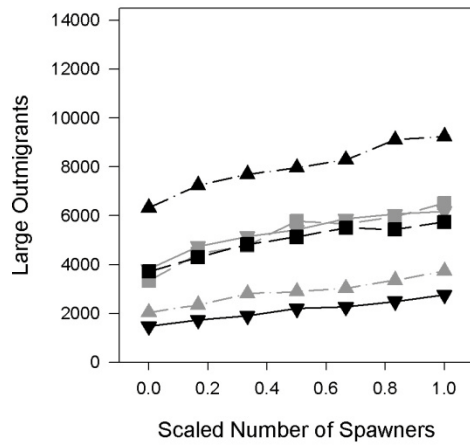
Figure 5. Simulation experiment results for base flow, food availability, and hiding cover availability. X axes represent the relative magnitude of the management variable, scaled 0-1 from lowest to highest values. Variable ranges are: base flow from -2 to +4 m³/s added to actual flows, food availability from 50% to 200% of calibrated values, and hiding cover from 50% to 150% of standard values. Y axes are the total number of large outmigrants over the 5 simulated years.
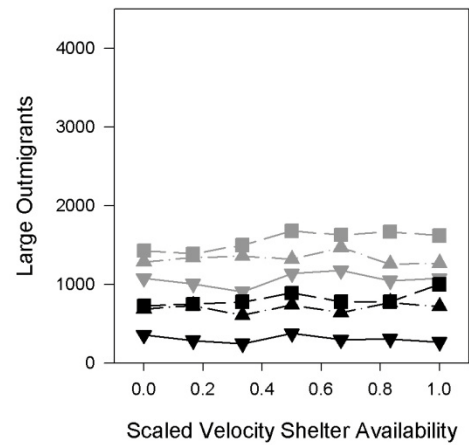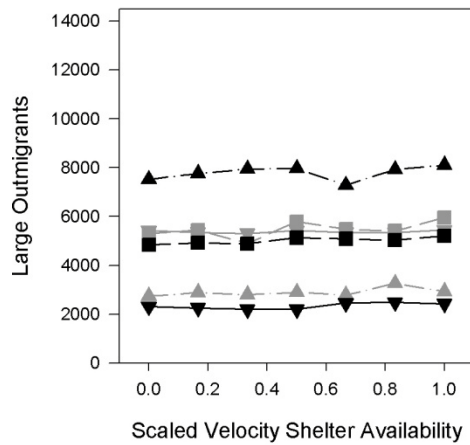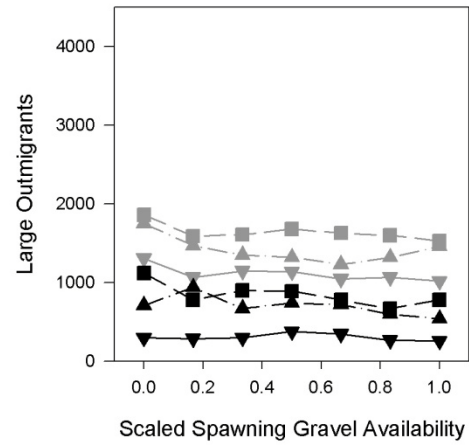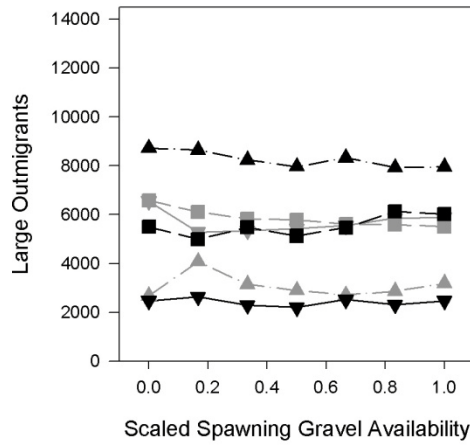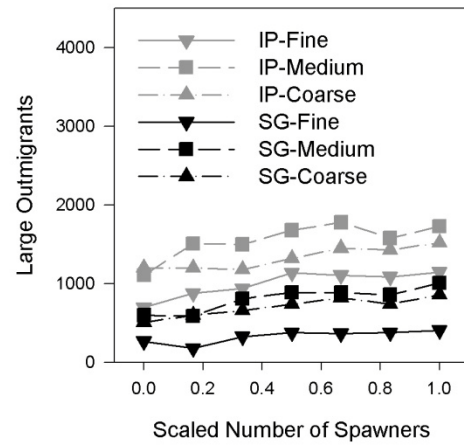
Figure 6. Simulation experiment results for number of spawners, spawning gravel, and velocity shelter availability. Variable ranges for all 3 experiments are from 50% to 150% of standard values.
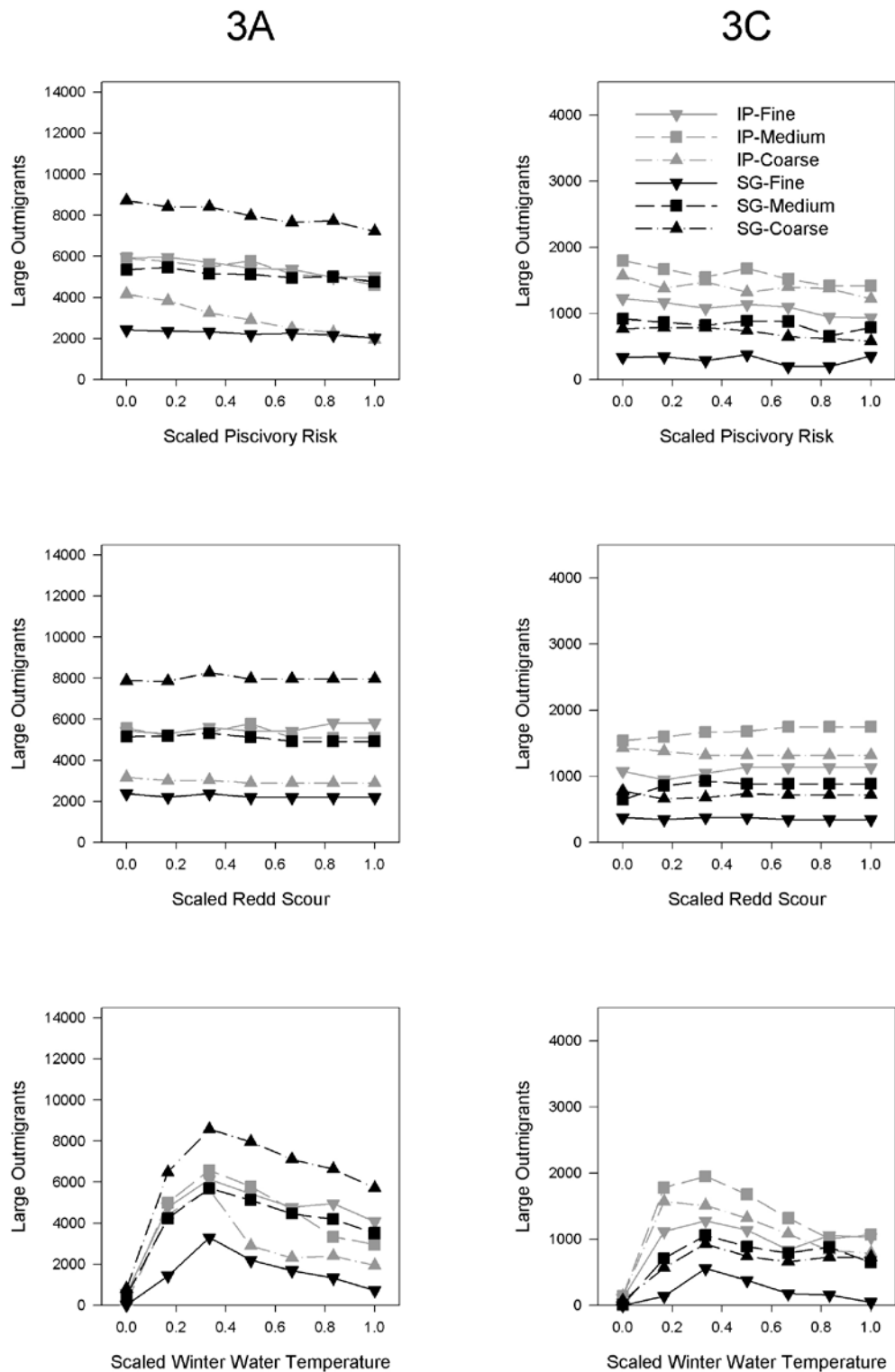
Figure 7. Simulation experiment results for piscivory risk (daily risk varied from 90% to 110% of standard value), redd scour (redd depth varied from 50% to 150% of standard), and winter temperature (November-May temperatures varied from -4 to +4°C).

For many of the experiments, scenarios P-FINE, P-MED, and S-MED produced results very similar in magnitude at site 3A, where habitat is relatively diverse. At the more uniform site 3C, the square grid cell scenarios consistently produced fewer large outmigrants than did the polygon scenarios. At 3C, the square cells produced much less area of very low depth and velocity (Figure 4), which could be critical for survival of newly emerged salmon fry.

The differences in results among the resolution scenarios appear to result from three processes discussed in Section II.B. First is the effects of spatial resolution on superimposition mortality of redds. At site 3A, superimposition mortality decreased as resolution decreased, so the number of fry produced increased consistently as resolution decreased from fine to coarse. At 3C, superimposition mortality was nearly equal between the medium- and fine-resolution scenarios but lower at coarse resolution; consequently, more fry were produced at coarse resolution. These differences are illustrated in Figure 8 for the irregular polygons scenarios and base flow experiment.
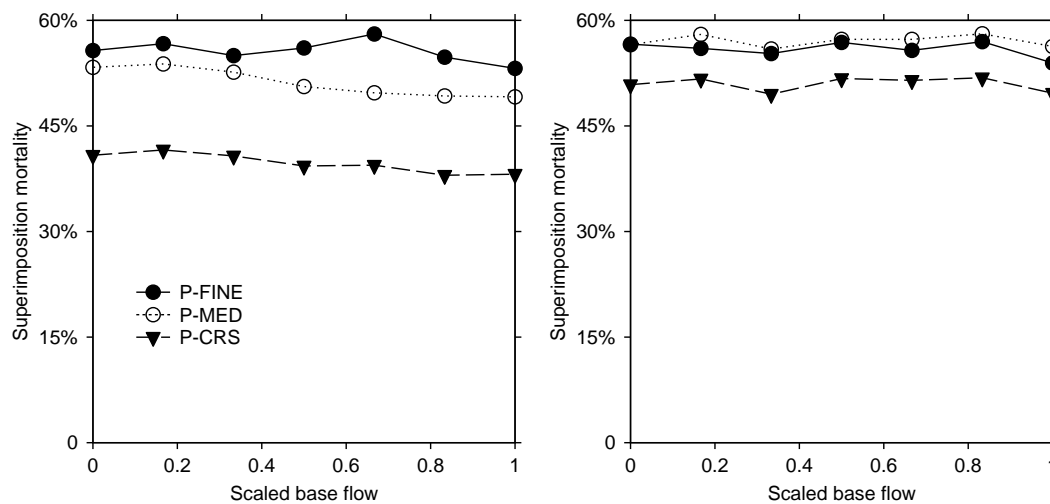

Figure 8. Superimposition mortality (percent of eggs lost to superimposition of new redds) under the three spatial resolution scenarios. Left: site 3A; right: site 3C. The plot depicts average mortality in the seven base flow scenarios (top row of Figure 5).

The second and third processes are decreased food competition and changes in area of especially good feeding habitat as resolution decreases, which can have counteracting effects. Using more and smaller habitat cells makes the model better able to reproduce the small areas of especially good habitat where real fish often feed; however, smaller cells can exaggerate the effects of food competition among the simulated superindividuals. The effects of these processes are illustrated by examining the percentage of fry that survive and stay in the modeled sites until reaching 5 cm length (Figure 9). This percentage is especially low for the coarse-resolution scenario, likely a result of the model being too coarse to represent small areas of especially good habitat. But the percentage was also lower for fine resolution than for medium, presumably because of the food competition process. The medium resolution appears to offer the best tradeoff between these two processes for a superindividual size of 10.
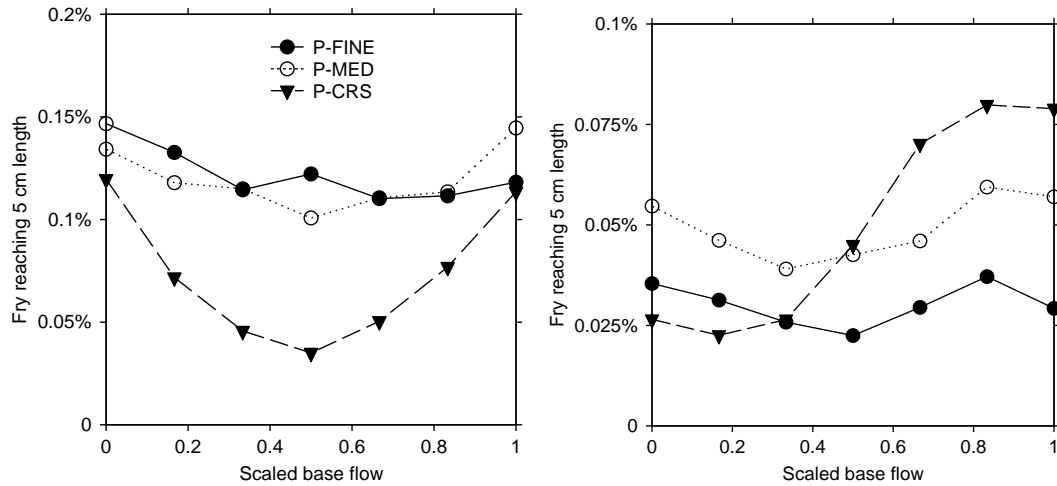
Figure 9. Percentage of fry surviving and reaching 5 cm fork length in the irregular polygon base flow experiment. Left: site 3A; right: site 3C. The plot depicts averages from each of the base flow scenarios (top row of Figure 5).

We expect the food competition process to depend on the superindividual size, because the superindividual size directly affects how much space is needed to support simulated juveniles. The superindividual size experiment (Figure 10) indicates that superindividual size has only a small effect at a value of 10 (results for superindividual size = 10 are quite similar to those for a size of 1). At the highest superindividual size of 50, the number of large outmigrants is strongly reduced, especially in the fine-resolution scenario, indicating that interactions due to food competition are strong. These results indicate that when superindividual size is 10, food competition is a partial but not major cause of differences among the resolution scenarios.
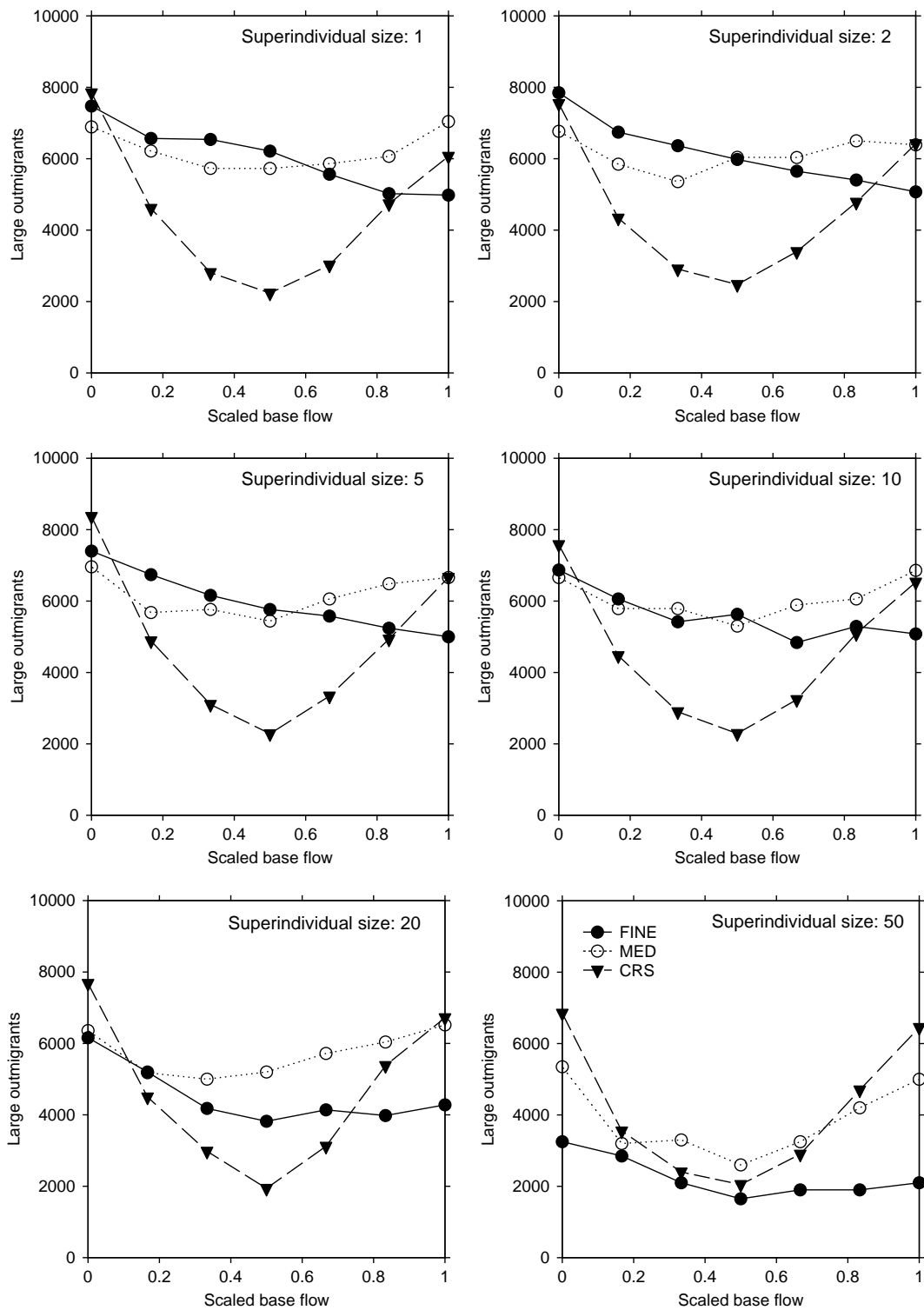
Figure 10. Results of the superindividual size experiment.

IV. Discussion and Conclusions

Our results indicate that several processes cause inSALMO's predictions of large outmigrant production to differ with how space is represented, and that the importance of some processes can differ among sites. At site 3A, which is larger and has habitat that varies more—but relatively gradually—over space, medium-resolution polygons and medium-resolution square cells produced results quite similar to those of fine-resolution polygons. At site 3C, where habitat is more uniform and pockets of especially good juvenile rearing habitat are smaller and more isolated, medium-resolution polygons produced results similar to those of fine-resolution polygons but none of the square-cell scenarios did.

One process clearly causing the differences among resolution scenarios is the reduced ability of larger cells to represent the relatively rare but important areas of low-depth and low-velocity habitat. This kind of habitat is especially important for inSALMO because it provides high survival and growth of newly emerged juvenile salmon. The loss of low-depth and low-velocity habitat area with increasing cell size is much worse for square cells than for irregular polygons because our polygons were carefully shaped to retain as much habitat variation as possible.

The sensitivity of inSALMO's redd superimposition submodel to cell size also appears to have strong effects at the Clear Creek sites, where superimposition is the dominant cause of simulated egg mortality. This sensitivity could probably be reduced by introducing some uncertainty in the simulated spawners' ability to identify the best possible cell for spawning. The current formulation assumes spawners perfectly sense which cell offers highest "suitability" and therefore concentrates spawning in those cells. Adding some randomness to this sensing ability may reduce superimposition rates and make them less sensitive to cell size.

Competition for the food in a cell also causes some effects of spatial resolution, and those effects interact, predictably, with the juvenile superindividual size. Smaller cells require smaller superindividuals to avoid food competition artifacts, with negative consequences to computational feasibility. Our analyses indicated that representing 10-20 juveniles per superindividual had little effect when fine- and medium-resolution irregular polygons were used.

Overall, our analyses indicate that medium-resolution irregular polygons combined with a superindividual size of 10-20 provide a good compromise between computational demand and model accuracy. Our medium-resolution polygons averaged about 25 m^2 in area but were much smaller in areas such as channel margins where gradients in habitat are especially steep and important to juvenile salmon. Square cells of approximately 4 m width also appear capable of producing relatively accurate results (compared to fine-resolution polygons) at sites where habitat conditions vary relatively gradually over space.

V.   References

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